Nitrogen leaching from N limited forest ecosystems: the MERLIN model applied to Gårdsjön, Sweden

O. J. Kjønaas, R. F. Wright

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O. Janne Kjønaas[1] and Richard F. Wright[2]

[1] Norwegian Forest Research Institute, Høgskoleveien 12, N-1432 Aas, Norway
[2] Norwegian Institute for Water Research, Box 173 Kjelsås, 0411 Oslo, Norway

Abstract

Chronic deposition of inorganic nitrogen (N) compounds from the atmosphere to forested ecosystems can alter the status of a forest ecosystem from N-limited towards N-rich, which may cause, among other things, increased leaching of inorganic N below the rooting zone. To assess the time aspects of excess N leaching, a process-oriented dynamic model, MERLIN (Model of Ecosystem Retention and Loss of Inorganic Nitrogen), was tested on an N-manipulated catchment at Gårdsjön, Sweden (NITREX project). Naturally generated mature Norway spruce dominates the catchment with Scots pine in drier areas. Since 1991, ammonium nitrate (NH_4NO_3) solution at a rate of about 35 kg N ha^{-1} yr^{-1} (250 mmol m^{-2} yr^{-1}) has been sprinkled weekly, to simulate increased atmospheric N deposition.

MERLIN describes C and N cycles, where rates of uptake and cycling between pools are governed by the C/N ratios of plant and soil pools. The model is calibrated through a hindcast period and then used to predict future trends. A major source of uncertainty in model calibration and prediction is the paucity of good historical information on the specific site and stand history over the hindcast period 1930 to 1990. The model is constrained poorly in an N-limited system. The final calibration, therefore, made use of the results from the 6-year N addition experiment. No independent data set was available to provide a test for the model calibration.

The model suggests that most N deposition goes to the labile (LOM) and refractory (ROM) organic matter pools. Significant leaching is predicted to start as the C/N ratio in LOM is reduced from the 1990 value of 35 to <28. At ambient deposition levels, the system is capable of retaining virtually all incoming N over the next 50 years. Increased decomposition rates, however, could stimulate nitrate leaching losses. The rate and capacity of N assimilation as well as the change in carbon dynamics are keys to ecosystem changes. Because the knowledge of these parameters is currently inadequate, the model has a limited ability to predict N leaching from currently N-limited coniferous forest ecosystems in Scandinavia. The model is a useful tool for bookkeeping of N pools and fluxes, and it is an important contribution to further development of qualitative understanding of forest N cycles.

Introduction

Chronic deposition of inorganic nitrogen (N) compounds from the atmosphere to forested ecosystems can lead to changes in ecosystem structure and function and to increased loss of N to runoff. Alterations in N cycling can move the ecosystem from an N-limited towards an N-rich system, in which the availability of ammonium and nitrate exceeds the total combined plant and microbial nutritional demand (Aber *et al.*, 1989). Critical ecosystem processes change and may lead to low ratios of gross (nitrate) NO_3 and (ammonium) NH_4 immobilisation to gross mineralisation, low soil C/N ratio, high foliar N concentration and high foliar N/lignin ratio. In addition, N-rich systems may leach inorganic N below the rooting zone and so increase concentrations of nitrate in surface waters (Aber, 1992; Stoddard, 1994; Gundersen *et al.*, 1998).

Forest ecosystems in Scandinavia are generally N limited, with leaching losses in the order of 7–35 mmol N m^{-2} year^{-1} (Binkley and Högberg, 1997). Along the southern coast of Sweden, however, NO_3 outputs from some forests approach rates of N input, while other forests in the same area show negligible rates of NO_3 leaching (Binkley and Högberg, 1997). If losses of organic and inorganic N are low, long-term elevated atmospheric N deposition could gradually eutrophy the system, with a build-up of N in soil and vegetation. Gradually, an ecosystem change and increased N leaching may result.

Predicting the amount and number of years of N deposition that a given forest ecosystem can tolerate before increased and persistent N leaching occurs is essential for the determination of critical loads for N for forests and surface waters. Models are commonly used to obtain such predictions. For example, relationships between inputs and outputs of N to forest ecosystems indicate that forests receiving >25 kg N ha^{-1} yr^{-1} (175 mmol m^{-2} yr^{-1}) have significant N outputs; outputs vary for forests receiving inputs 10–25 kg N ha^{-1} yr^{-1} (70–175 mmol m^{-2} yr^{-1}); and outputs are low for inputs <10 kg N ha^{-1} yr^{-1} (70 mmol m^{-2} yr^{-1}) (Dise and Wright, 1995). However, such empirical relationships do not indicate the time required for an ecosystem to move from an N-limited to a 'N-saturated' state at a given rate of N deposition. Deterministic, process-oriented dynamic models may provide information on the time aspects of excess N leaching. A recently developed model, MERLIN (Model of Ecosystem Retention and Loss of Inorganic Nitrogen, (Cosby *et al.*, 1997)), aims to provide such a tool.

Large-scale, whole ecosystem experiments such as the NITREX project (NITRogen saturation EXperiments) provide key information for development and testing of predictive models. NITREX comprises 11 experiments at 7 sites in Europe at which N deposition to whole ecosystems has been changed experimentally and the response of vegetation, soils and waters investigated (Wright and van Breemen, 1995; Emmett *et al.*, 1998). One of the NITREX sites is located at Gårdsjön, near Gothenburg, Sweden. Here, the ambient N deposition of 12 kg N ha^{-1} yr^{-1} (85 mmol m^{-2} yr^{-1}) is increased to about 50 kg N ha^{-1} yr^{-1} (350 mmol m^{-2} yr^{-1}) by weekly additions of NH_4NO_3 to the forest floor (Wright *et al.*, 1995). Intensive investigation of vegetation (Kjønaas *et al.*, 1998), soil N processes (Kjønaas *et al.*, 1998), soil solution (Stuanes and Kjønaas, 1998) and runoff (Moldan and Wright, 1998) during the 2 years prior to and 6 years of treatment provide a comprehensive data set for the application of MERLIN.

The objectives of this paper are (1) to evaluate the potential of the model to predict future N leaching from a N-limited forested ecosystem with (a) current and increased levels of anthropogenic N input, and (b) different scenarios of organic matter decomposition, and (2) to identify knowledge that may improve the predictability of ecosystem change from N-limited to N-rich.

Description of MERLIN

MERLIN is a simple process-oriented model designed to simulate and predict concentrations of inorganic N in soil leachate and runoff in terrestrial ecosystems (Cosby *et al.*, 1997). The model links C and N cycles. The ecosystem is simplified to 2 plant compartments (active biomass such as foliage and roots and less active structural woody biomass) and 2 soil compartments (labile and refractory organic matter) and functions at annual time steps (Fig. 1). The C pools and fluxes are inputs to the model; N pools and fluxes are linked to C by C/N ratios in the pools. Transfer of C and N between compartments occurs by processes such as plant uptake, litterfall, immobilisation, mineralisation, nitrification and denitrification. No feedback occurs between N status and C fluxes; the rates of these processes are assumed to be governed by C/N ratios in the various pools. MERLIN comprises (1) a book-keeping procedure in which inputs and outputs of C and N to the ecosystem and between the 4 compartments are tallied, and (2) a series of simultaneously-operating processes that describe the transfer of C and N between the compartments and out of the ecosystem.

MERLIN treats N dynamics as follows: N inputs can be atmospheric deposition, fertiliser and N fixation. Time series of all inorganic N inputs are specified *a priori*. Nitrification, microbially mediated transformation of NH_4 to NO_3, is represented in the model by a first-order reaction. Adsorption of NH_4 on the soil matrix is modelled as a non-linear capacity-limited process using a Langmuir isotherm approach. N losses from the system are as inorganic (DIN) and organic (DON) N in runoff and as gases (N_2O and N_2) from denitrification.

Plant biomass represents the aggregated pool of C and N present in the active portion of the ecosystem. The time series of net productivity is determined from specified time sequences of plant biomass, litter production and long-term storage such as wood production. Plant growth requires N uptake from the soil as NH_4 and NO_3. Uptake is modelled as a non-linear Michaelis-Menten process that depends on the soil water concentration of NH_4 or NO_3. The maximum uptake rate is assumed to be proportional to the net primary productivity of the plants.

Soil organic material is divided into two compartments: labile organic matter (LOM) and refractory organic matter (ROM). Each is an aggregated pool of C and N representing accumulated organic compounds in the ecosystem. These materials provide the energy substrate for soil microorganisms, which immobilise and mineralise C and N in soils. Microbial immobilisation of inorganic N is modelled as a non-linear Michaelis-Menten process that depends on the concentration of NH_4 or NO_3 in soil solution. The maximum immobilisation rate is assumed proportional to microbial secondary productivity.

Litter from the plant compartment enters the LOM pool. C and N leave this pool by decomposition (transformation of organic C to CO_2) and decay (degradation of the quality of the organic material). The decay products are passed on to the ROM pool. Additional C and N leave ROM by decomposition. The model requires input information for litter production, the size of the carbon pool stored in LOM and the decomposition of LOM at each time step. In addition, the size of the carbon pool stored in ROM is required. The decomposition of ROM is calculated by difference from the C budgets.

Inputs required for MERLIN are temporal sequences of (1) C fluxes and pools, (2) hydrological discharge, and (3) external sources of inorganic N. Initial conditions (amounts of C and N) must be specified for each compartment. Several 'constants' (e.g. uptake parameters) are needed to specify the N dynamics of the organic compart-

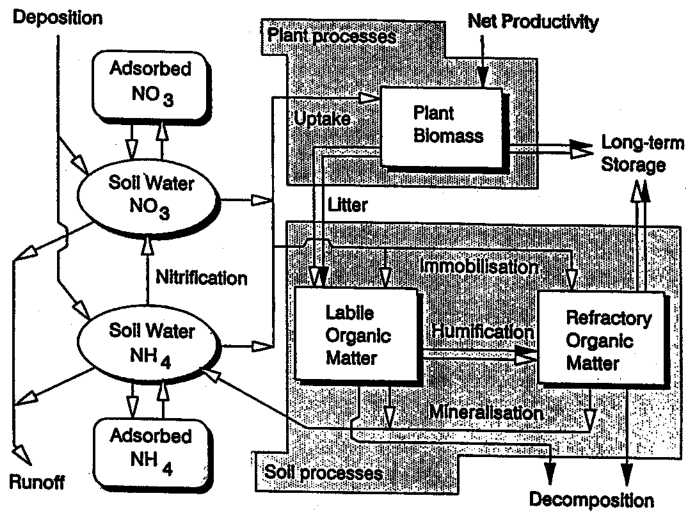

Fig. 1. *The conceptual basis of the MERLIN model. Closed arrows represent fluxes of inorganic C; open arrows represent fluxes of inorganic M. Pair closed/open arrows represent fluxes of organic matter containing both C and N. From Cosby et al. (1997).*

ments, and characteristics of the soils must be given (depth, porosity, bulk density, anion/cation exchange characteristics).

Outputs from MERLIN include: (1) concentrations and fluxes of NH_4 and NO_3 in soil water and runoff; (2) total N contents of the various compartments; (3) the C/N ratios of the aggregated plant and soil compartments; and (4) estimates of processes in the N cycle such as uptake, gross mineralisation and immobilisation. Further details are found in Cosby *et al.* (1997).

Site description and experimental design

SITE DESCRIPTION

The experimental site at Gårdsjön is located at 135–145 m elevation about 10 km from the Swedish west coast (58 04′N, 12 01′E), 50 km north of Gothenburg. The Gårdsjön region has a humid climate, with 1100 mm mean annual precipitation, 586 mm mean annual runoff and mean annual temperature of 6.4°C. The area is characterised by an acid lake (pH 4.7, Olsson *et al.*, 1985) whose terrestrial catchment is dominated by shallow podsolic soils with inclusions of barren rock and peaty soils. The bedrock consists mainly of granites and granodiorites (Olsson *et al.*, 1985).

The N-manipulated catchment (G2 NITREX) has an area of 0.52 ha. The forest is mainly naturally regenerated, uneven-aged Norway spruce (*Picea abies* L. Karst) with some Scots pine (*Pinus sylvestris* L.) in dry areas. The mean age was 104 years in 1991. Ground vegetation is dominated by dwarf shrubs and mosses, mainly *Vaccinium myrtillus* L., *Vaccinium vitis-idea* L., *Dicranum majus* Sm., and *Leucobryum glaucum* (Hedw.) Fries, in the upper catchment, *Sphagnum*, (predominantly *Sphagnum girgensohnii* Russ.) and *Vaccinium myrtillus* L. in the wetter lower parts, and heather (*Calluna vulgaris* (L.) Hill) among the drier outcrops and the most exposed ridges (Stuanes *et al.*, 1992; Nygaard *et al.*, 1993).

Soils are predominantly acidic silty and sandy loams, drier in the upper catchment and more peaty in the lower parts. They are classified as Orthic Humic Podzols, Orthic Ferro-Humic Podzols, Gleyed Humo-Ferric Podzols, and, at the shallow outcrops, Typic Folisols (Canadian system of soil classification, 1978). The C/N ratio ranges from 32 to 52 in the organic horizon. Soil depth ranges from 0 cm to more than 100 cm with an average of 38 cm (Kjønaas *et al.*, Stuanes *et al.*, 1992).

The Gårdsjön area receives moderately high deposition of sulphate, nitrate and ammonium; 14-year mean (minimum and maximum) throughfall inputs at a nearby catchment (CONTROL) for 1979–1992 were 83.0 (36.3 to 105.3) mmol sulphate (SO_4-S) m^{-2} yr^{-1}, 52.1 (32.8 to 83.6) mmol NO_3-N m^{-2} yr^{-1} and 34.3 (17.1 to 55.0) mmol NH_4-N m^{-2} yr^{-1}, respectively (Moldan *et al.*, 1995).

EXPERIMENTAL DESIGN

Increased atmospheric deposition of N was simulated, starting in April 1991, by weekly experimental additions of NH_4NO_3 solution at a rate of about 250 mmol N m^{-2} yr^{-1} (35 kg N $ha^{-1}yr^{-1}$). NH_4NO_3 was dissolved in de-ionised water and applied by means of 270 ground-level sprinklers installed in a 5×5 m grid over the whole catchment. Additions were done weekly in amounts proportional to the volume of ambient throughfall which occurred the previous week. The additional water comprised about 5% of total throughfall volume. The average NH_4NO_3 addition was in 1.4 mm of water and added during 30 minutes. This amount and intensity was chosen such that hydrological discharge was not affected on an event or an annual basis (Wright *et al.*, 1995).

Methods and data for the forest G2 NITREX 1990 and 1930

POOLS 1990

Trees and ground vegetation

The total standing tree biomass was determined using Marklund's biomass functions for pine and spruce separately (Marklund, 1988), with diameter at breast height (dbh), height of the trees, height to the lowest green branch and site index as inputs (Kjønaas *et al.*, 1998). The various components were divided into a structural component and an active component. The active component was calculated as the sum of needles, twigs (1/3 of total branch estimates), and fine roots less than 5 mm. The calculated fine root (<5 mm) was 3 times the fine root biomass (<1 mm) reported by Clemmensson-Lindell and Persson (1995). The structural component was calculated as total biomass minus the active component. Total biomass in 1990 was estimated at 15.5 kg m^{-2}; 2.4 for the active crown and root pool and 13.1 for the structural wood pool. Foliage was collected once a year in the autumn from the 7th whorl from the top of the tree. The needles from each branch were sorted by age and analysed for total N. Six spruce trees from each of the three vegetation and soil types in G2 were sampled together with six pine trees.

No biomass data were available for the ground vegetation in the G2 NITREX catchment. An estimate of the ground vegetation C and N pools was derived from measurements at a 250-year-old Norway spruce stand in northern Finland (Havas and Kubin, 1983) combined with N contents from ground vegetation in the G2 NITREX catchment. The ground vegetation of the Finnish site was dominated by mosses and dwarf shrubs (311 and 282 g m^{-2}, respectively), with *Vaccinium myrtillus* L. dominating among the dwarf shrubs (178 g m^{-2}). The ground vegetation was assumed to be in steady state, with annual production equal to annual litterfall. The total ground-layer vegetation amounted to 541 g m^{-2} and the below-ground root biomass 1290 g m^{-2}. The ground vegetation was treated as part of the active plant pool and was added to the active tree pool. Assuming 50% C in biomass, the total C pool of the active plant compartment was thus 1759 mol m^{-2} and 546 mol m^{-2} for the structural wood compartment. Total yearly increment of the structural wood pool was calculated from measured differences in biomass between 1990 and 1994, amounting to 6.87 mol C m^{-2}. The N pool was 1.58 mol m^{-2} for the active tree compartment and 1.31 mol m^{-2} for the ground vegetation; a total of 2.89 mol m^{-2} for the active plant pool. The structural wood compartment contained 1.62 mol N m^{-2} (Fig. 2, Table 1).

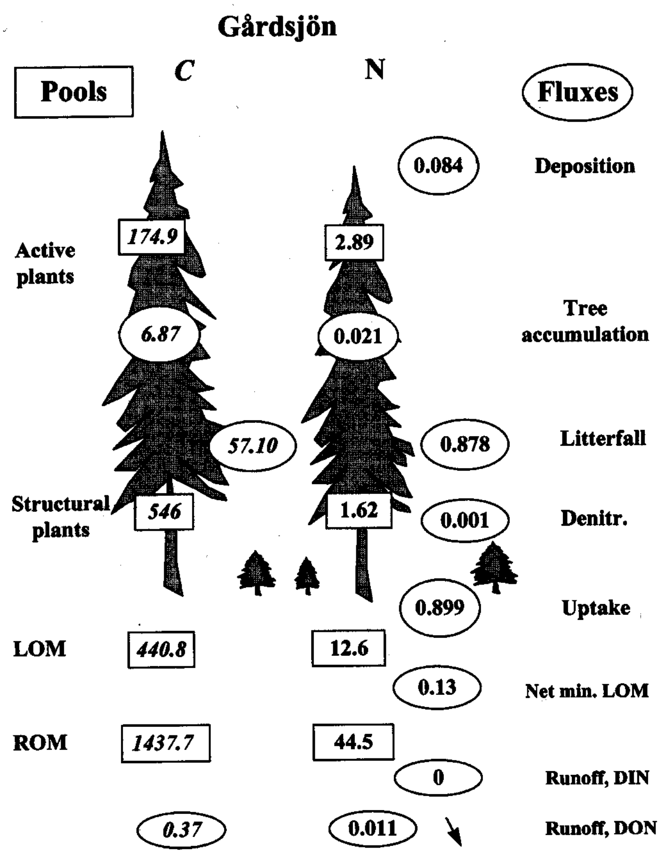

Fig. 2. *C (italics) and N (bold) pools (mol m^{-2}) and fluxes (mol m^{-2} yr^{-1}) in the G2 NITREX catchment, Gårdsjön, Sweden, in the reference year 1990. The active plant pool is the sum of the active tree pool (measured and calculated by use of Marklund's biomass models; Marklund, 1988) and the ground vegetation (estimated). The litter C and N fluxes is the sum of tree litter (measured) and ground vegetation litter (estimated). Uptake is calculated from wood increment (measured) and litter. Deposition and runoff from Moldan and Wright (1998), net mineralisation from Kjønaas et al. (1998), denitrification from Klemedtsson et al. (1997).*

Soil

Soil organic matter consists of material with decomposition times ranging from days to thousands of years. The MERLIN model simplifies the soil organic matter into 2 fractions: a fraction with relatively rapid turnover time termed 'labile organic matter' (LOM) and a fraction with longer turnover time, termed 'refractory organic matter' (ROM). The LOM pool provides a compartment that can respond rather quickly and is most readily identified with the forest floor in forest ecosystems, while the ROM pool represents the bulk of carbon and N down through the B and C horizons (Cosby *et al.*, 1997). Although both labile and refractory organic matter are dispersed throughout the soil both vertically and horizontally, in general, litter and forest floor consist of more-rapidly decomposed material, whereas organic matter in deep soil layers consists of older material with slower turnover times. For this model appli-

Table 1. Pools of active plant compartment, labile organic matter (LOM) and refractory organic matter (ROM), and flux of N in runoff for the years 1930 (assumed), 1990 (measured/calculated, and calibrated), 1995 (measured/calculated, and calibrated) and 2040 (predicted) for the G2 NITREX plot subjected to increased N input from 1991. [1]No change in needle N content and needle weight between 1990 and 1995, no data available for ground vegetation, [2]* significant difference between 1990 and 1995 (Wilcoxon signed rank test, p=0.04) . [3] Thickness of horizons and carbon content as 1990. [4] Difference between 1990 and 1995 was not significant (p=0,39).

			1930 assumed	1990 measured/ calculated	1990 calibrated	1995 measured/ calculated	1995 calibrated	2040 predicted
Pools	Active plants	C	174.9	174.9	174.9		174.9	174.9
(mol m^{-2})		N	2.86	2.89	2.89	2.89[1]	2.93	3.0
		C/N	61.1	60.5	60.5		59.7	58.6
	LOM	C	429.3	440.8	440.8		440.8	440.8
		N	11.3	12.6	12.6	13.0[2]*	13.8	18.2
		C/N	38.0	35.0	35.0	33.9[3]	32.1	24.3
	ROM	C	1437.5	1437.7	1437.7		1438.7	1447.2
		N	44.3	44.5	44.5	50.0[4]	44.9	51.4
		C/N	32.5	32.3	32.3		32.1	28.2
Fluxes								
(mmol m^{-2} $year^{-1}$)	Runoff		0	0	0.46	13	1.05	205.5

cation, LOM was defined as the soil organic matter in the forest floor (L, F and H horizons). Thick Oh horizons located in the wet *Sphagnum* area of the catchment, however, were considered part of the ROM pool, along with the organic matter in the mineral horizons. The presence of smaller amounts of older humified organic matter in the forest floor and some rapidly decomposable fine root litter in the mineral horizon was ignored. Most of the fine roots were found in the forest floor. Soil samples were taken in a grid across the catchment, every 5×10m for the humus layer and every 10×10m for the mineral soil to quantify the pools and the soil chemical variability in the catchment. The pool of LOM was based on a mean depth of 11 cm, bulk density of 134.8 kg m^{-3}, 86% loss on ignition of which 50% is assumed to be C, and 1052 mmol N kg^{-1} soil. The pool of ROM was calculated using a mean depth of 27 cm, bulk density of 722 kg m^{-3}, 17.7% loss on ignition of which 50% is C, and 228.5 mmol N kg^{-1} soil. This gave C and N pools of LOM of 440.8 and 12.6 mol m^{-2}, ROM of 1437.7 and 44.5 mol m^{-2} (Fig. 2), and C/N ratios for the LOM and ROM pools of 35.0 and 32.3, respectively (Table 1).

FLUXES 1990

Input-output

Atmospheric inputs were measured by two bulk precipitation collectors and 28 throughfall collectors. Samples for chemical analysis were collected and bulked to one sample biweekly or monthly. Runoff from the G2 NITREX catchment was gauged continuously. Runoff samples for chemical analysis were collected weekly or biweekly as flow-proportional samples (grab samples prior to November 1991). The mean N deposition for pre-treatment years 1989–90 was 84 mmol N m^{-2} yr^{-1} (sum of wet precipitation and dry deposition). The measured output of DIN in runoff was <0.5 mmol m^{-2} yr^{-1}, while the loss of DON was 11 mmol m^{-2} yr^{-1} (Fig. 2) (Moldan *et al.*, 1995).

Litterfall

Litter from trees was sampled monthly from 23 collectors arranged in five rows near the throughfall samplers. Samples were bulked according to vegetation and soil moisture regime, dried, sorted (spruce needles, pine needles, cones and 'rest') and weighed. The samples were analysed quarterly. Litter flux from the trees was calculated as the sum of mean aboveground litterfall for 1990 and 1991 (11.7 mol C m^{-2} yr^{-1}; 187 mmol N m^{-2} yr^{-1}) (Kjønaas *et al.*, 1998) and a below-ground yearly litter production equal to the measured fine-root biomass (<1 mm) down to 30 cm depth, of 220 g m^{-2} (Clemmensson-Lindell and Persson, 1995). This gave a total C litter flux from trees of 22.8 mol m^{-2} $yr^{-1}$and a weighted C/N ratio of 69.8. For the assumed steady-state ground vegetation, above-ground litterfall was set equal to the regrowth, which amounted to 177 g m^{-2} (Havas and Kubin, 1983). Assuming 50% of root biomass as annual below-ground litter production resulted in a total ground vegetation biomass of 1369 g m^{-2}, a C litter flux of 34.3 and a C/N ratio of 62.1. The total litter C flux was thus 57.1, with a C/N ratio of 65.

Soil N transformation processes and decomposition

Net mineralisation and denitrification have been measured *in situ* in the G2 NITREX catchment. Denitrification rates were determined using a closed-chamber technique with three chambers placed in each of the three soil moisture regimes. The net N_2O production was 1 mmol m^{-2} yr^{-1} in the period 1993 through 1994 (Klemedtsson *et al.*, 1997). The rate was of minor importance for the total N budget and was thus not included in the model simulations. A soil-core incubation technique was used to measure the rate and amount of microbiological conversion of organic-N to NH_4 (ammonification) and NH_4 to NO_3 (nitrification). Net N mineralisation is the sum of net ammonification and net nitrification. Incubations were done *in situ* in 3 plots under different ground vegetation and moisture regimes, by means of the resin-core technique (DiStefano and Gholz, 1986; Kjønaas *et al.*, 1998). Soil cores were sampled using 15-cm long PVC tubes and incubated with mixed-bed ion-exchange resin bags in the bottom of the core. Ten replicates were deployed at each plot over 2-month intervals during the growing season (May–June, July–August, September–October) and over 6 months during the winter (November–April) between 1991 and 1993. The major part of the incubated soil samples consisted of forest floor (LFH) material, which reflects the net mineralisation of the LOM pool. The net mineralisation of 1991 served as the measured net mineralisation rate for 1990 (Fig. 2). Limited data are available for *in situ* decomposition and accumulation of organic matter in the LOM and ROM pool of the G2 NITREX catchment. The ROM pool was assumed to be in steady state, while 0.2% of the litter input was assumed to accumulate annually in the LOM compartment. Decomposition in LOM was set to 50.8 mol C m^{-2} yr^{-1} and the decomposition of ROM was set to 5.74 mol C m^{-2} yr^{-1}.

CHANGES IN POOLS AND FLUXES FROM 1930 TO 1990

The year 1930 was chosen as the starting point for the model application. At this time, the forest was well established and the N deposition was much lower than today. Little information is available on the specific site and stand history over the period 1930 to 1990. The area surrounding Lake Gårdsjön has supported a low level of grazing and extensive forestry for centuries, with major cutting of some areas in 1904 (Olsson, 1985). Since the mean age of the trees in G2 NITREX catchment was 104 years in 1991 (Kjønaas *et al.*, 1998), there probably was only limited harvesting during the past decades.

Reliable time trends are generally available only for bole production in forests, while data are sparse on development of the active crown compartment, variation in litterfall and the build-up of soil organic matter within a rotation cycle of a forest. The wood increment between 1930 and 1990 was assumed to be lower than the measured increment in the structural plant pool between 1990 and 1994 (Fig. 1). The relatively large increment found in the period from 1990 to 1994 encompasses four years of increased N addition which may have increased the wood production. The measured increment was slightly larger than increments given in production forestry yield class tables for *Picea abies* with similar site index, stand density, and age (Braastad, 1975). This yield table was based on planted forests with 3 thinnings and a relatively intensive management. The time sequence for wood production in the uneven-aged, naturally-regenerated forest of the G2 NITREX catchment was assumed lower than the planted forests represented in the forestry yield class tables. Thus, the structural plant pool was assumed to increase from 3.5 to 4.4 mol C m^{-2} yr^{-1} between 1930 and 1990 (Table 2).

Table 2. Relative change in deposited NH_4-N and NO_3-N, and relative change in the labile organic matter pool (LOM) and the wood pool for the hindcast period 1930—1990. The mean reference input for 1989 and 1990 was 42 mmol m^{-2} for both NH_4-N and NO_3-N.

Year	NH_4-N	NO_3-N	LOM	Wood
1930	0.38	0.1	0.974	0.57
1950	0.5	0.2	0.988	0.70
1970	1		0.994	0.84
1975	1	0.9		
1990	1	1	1	1

The increment of the active 'crown' pool was expected to be stable or slightly declining from canopy closure and onwards (Albrektson, 1980). The forest was assumed to have reached canopy closure at the starting point for the model application, as the mean stand age in 1930 was 44 years. Despite a slight increase in the active crown pool estimated by Marklund's biomass models (Marklund, 1988) between 1990–94, the active tree pool was treated as being in a steady-state in this model simulation. As the active plant pool was considered to be in a steady state, the litter production was also assumed constant over time from 1930 to 1990.

The organic matter in the forest floor (LOM) was assumed to go through some changes, with a slow build up of the forest floor (Table 2) by means of a balance between build-up of C from litterfall and a slow increase in decomposition/mineralisation over the period. Although mineralisation decreases with increasing soil depth (Persson and Wirén, 1995), some mineralisation was assumed to take place in the ROM compartment. As the N content in the mineral soil was found to be relatively constant between age 50 and 100 years of a forest (Sogn *et al.*, 1997) the decomposition of ROM was set close to the input of organic C from LOM, with only a minor increase in C and N between 1930 and 1990 (Table 1.)

The increase in NH_4-N and NO_3-N deposition between 1930 and 1990 has been assumed to follow separate trends (Table 2). The shape of the NH_4-N deposition curve has been coupled with the development of the S emissions between 1930 and 1975 (Mylona, 1996) while the NO_3 deposition follows the NO_x emissions trend given by Simpson *et al.* (1997).

Calibration procedure

Calibration of MERLIN firstly entails compilation of C and N pool and flux data (Fig. 2), along with time sequences of changes of pools and fluxes for the site at the present-day (termed reference year, here 1990) and at one or more points in time in the past. Generally, the model is run for 50–100 years starting at a point in time (termed background year, here 1930) at which the N deposition is low and constant. The model is then run for the hindcast period such that the present-day simulated C/N ratios of the active plant pool, the labile soil pool, the refractory soil pools, and the simulated losses of DIN in runoff, match those measured (Cosby *et al.*, 1997). This involves adjustment of the uptake parameters of plants, LOM and ROM (Table 3) to make the model fit the observations of the system.

Table 3. Uptake curves for the MERLIN model calibrated to the G2 NITREX catchment subjected to increased N addition from 1991. Optimum C/N (strength) determines the relative competitiveness of the plant, LOM and ROM pools to runoff. The higher the number, the less strongly N is taken up by plants or immobilized into the soil. The reference C/N is the C/N target to which the pool strives. The closeness of the pool's C/N ratio to the reference C/N is determined by the steepness of the curve, termed the C/N half width.

Uptake curves	
Plants	
opt. C/N (strength)	70
reference K2	1000
reference C/N (target)	57
C/N half width K2	0.3
LOM	
opt. C/N (strength)	32
reference K2	1000
reference C/N (target)	20
C/N half width K2	1.57
ROM	
opt. C/N (strength)	34
reference K2	1000
reference C/N (target)	28
C/N half width K2	0.54
C/N wood	336.2
C/N litter	65
Nitrification rate	1000

HINDCAST

There are many possible sets of parameters that will give a satisfactory fit to the measured 1990 data of the G2 NITREX catchment. Because very little happens with N cycling and fluxes in the forest ecosystem during the hindcast period 1930 to 1990, the model is poorly constrained. The calibration, therefore, made use of results from the 6 years of N addition (1991–1996). The assumptions that were made for the hindcast period 1930–90 were: (1) virtually all incoming N deposition is retained by the forest with little leakage; (2) N inputs are mostly retained by LOM, secondarily by ROM, while there is little change in the plant pool; and (3) the C/N ratio of LOM and plants decrease somewhat, while there is only minor change in ROM. In addition, the following criteria were set for the calibrated period 1989–1996, NITREX N addition experiment: (1) N leakage increases from <0.5 mmol NO_3 m^{-2} yr^{-1} to 10–20 mmol NO_3 m^{-2} yr^{-1}; (2) most of the added N is stored in LOM; (3) C/N ratio decreases in LOM with little or no changes in C/N of ROM and plants; and (4) increased mineralisation rates with increased N input as indicated by Kjønaas *et al.* (1998) and Falkengren-Grerup *et al.* (in press). Empirical data compiled from 35 coniferous forests in Europe were used to constrain the calibration further. The ECOFEE database (Gundersen *et al.*, in press) shows a close relationship between % N 'retention' (defined as output/input) and C/N ratio of forest floor. At C/N ratios above about 30, sites generally retain all incoming N, whereas at C/N ratios below 25, N retention is less complete. Long term predictions with continued increased N input were expected to fit the trend of the ECOFEE database for LOM C/N versus NO_3 leaching. No independent data were available to test the model prediction.

FORECAST

The calibrated model was used to predict N leaching given continued N addition at the NITREX rate or given N deposition at ambient 1990 rate. Precipitation followed the measured precipitation between 1989–1996, and was set constant thereafter (Fig. 3). The forecasts necessitate specification of future C pools. In the time trends for the forecast of the G2 NITREX catchment, the C/N of litter was expected to decrease, based on measurements of increased N in tree litter between 1990 and 1995 (Kjønaas *et al.*, 1998) (Table 4). The uptake parameters (Table 2), C/N for wood products, decay of LOM and ROM and soil organic export were kept constant at the 1990 level. Biomass for plants, wood and litter production is expected to change in relatively mature forests. As trees age, increased input of coarse woody litter such as large branches and dead tree boles is likely to occur, which may increase the C/N ratio of LOM and ROM. Limited data are available on the extent and amount of coarse woody

Table 4. Relative change in C/N of litter and different scenarios of decomposition of LOM and ROM for the forecast period 1991–2040. The scenarios are conservative assumptions based on observed net mineralization and decomposition at sites with different N input (Falkengren-Grerup *et al.*, 1998, Boxman *et al.*, 1998).

Treatment	Parameter		Year 1991	1995	2015	2040
N addition	Litter C/N		1	0.925	0.850	0.80
	Decomposition LOM	steady state	1	1	1	1
		reduced, –8%	1		0.95	0.92
		increased, + 8%	1		1.05	1.08
	Decomposition LOM and	LOM +8%,	1		1.05	1.08
	ROM	ROM –90%	1		0.9	0.1
Ambient N,	Litter C/N		1	1	1	1
(1990 level)	Decomposition LOM	steady state	1	1	1	1
		increased, + 8%	1		1.05	1.08
		increased +20%,	1		1.1	1.2
	Decomposition LOM and	LOM +20%,	1		1.1	1.2
	ROM	ROM –90%	1		0.9	0.1

debris in Scandinavian spruce forests. To simplify the model simulation, the biomass for plants and LOM, and the wood and litter production, were thus kept constant at the 1990 level. Different scenarios of organic matter decomposition were tested, including constant, reduced, and increased decomposition of LOM and ROM (Table 4). The scenarios are conservative assumptions based on observed net mineralisation and decomposition at sites

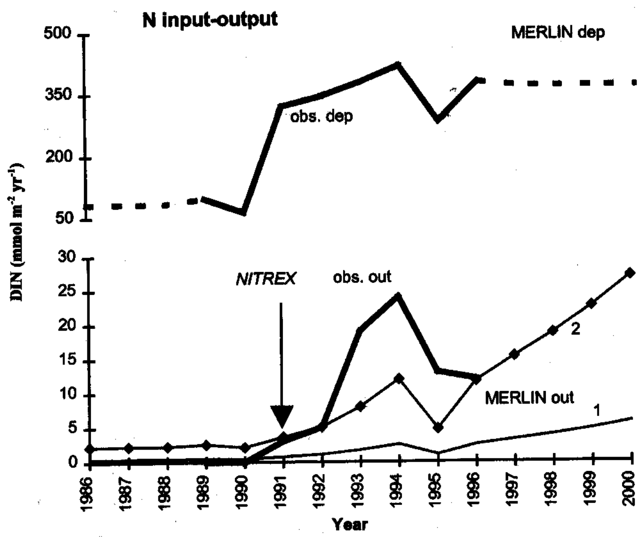

Fig. 3. *Deposition and runoff fluxes of inorganic N at the catchment G2 NITREX as measured (Moldan and Wright, 1998), calibrated (1989—1996) and simulated (1997–2000). The calibrated line 1 is based on zero leaching in 1989 and 1990, while the calibrated line 2 matches the observed output in 1991, 1992 and 1996. Note the different scale for deposition and runoff.*

with different N input (Falkengren-Grerup *et al.*, submitted; Boxman *et al.*, 1998).

Results and discussion

HINDCAST PERIOD

Hindcast

The reconstructed N cycle for the year 1930 at Gårdsjön G2 NITREX catchment reflects the assumption that the forest is aggrading slowly. The calibration suggests that as the forest grows slowly and matures during the 60-year period 1930–90, a small amount of N is stored in the boles of the trees (1.0 mol m^{-2}), and lost as dissolved organic N (DON) to runoff (0.7 mol m^{-2}). The forest floor is assumed to accumulate, and, thereby increase the N stored in LOM by 1.3 mol m^{-2}. The N required comes in part from N deposition (3.2 mol m^{-2}), via immobilisation and release of deposited N in the forest floor, and from decomposition of litter. Prior to the increased N input in the 1950's, a slight 'mining' of ROM took place to supply the N necessary for growth of the trees and to build forest floor. This mining of the mineral soil during a forest life cycle is probably a natural feature of boreal forests (Johnson, 1992) as is suggested by a study of N content in the soil profile under different ages of Norway spruce at Nordmoen, Norway (Sogn *et al.*, 1998). Most forests retain N very efficiently, such that in the absence of increased anthropogenic N deposition there is very little N entering the system and very little lost. However, limited information exists on fluxes within the forest ecosystem. As historical information is utilised to constrain the future behaviour of the model (Cosby *et al.*, 1997), the lack of good historical data on the development of a forest ecosystem is a major source of uncertainty in model calibration and hence of predictions of future trends.

Pools

The pool estimates for the reference year 1990 are combinations of measured, calculated and estimated data. For the soil data, the grid sampling gives a fairly good estimate of the C and N pools in the catchment. However, the partitioning of soil organic matter into the LOM and the ROM pools of the model is more difficult. LOM may represent the forest floor, or an accumulation of a number of years of litter. At the G2 NITREX catchment, the upper 3.5 cm LF layer sampled from incubated mineralisation cores during 1991 equalled 2.5 times the estimated litter input (142.7 mol C m^{-2}). This horizon may rightly be viewed as more labile than the forest floor as a whole. However, since pool data from the catchment level sampled in 1990 and 1995 as well as N transformation data from 1991 through 1993 were available only for the total forest floor, the forest floor was also chosen as the LOM compartment in the model run. The choice of the LOM pool affects estimates of future N leaching. As the LOM compartment is intended to provide a compartment that responds rather quickly, and any N assimilation connected to microbial growth is closely tied to the availability of substrate C, the size of the LOM pool affects the immobilisation of externally-added as well as internally-produced N.

Fluxes

The estimated ground vegetation biomass was large compared to the active tree compartment, mainly due to the large root pool in ground vegetation. Below-ground tree root biomass <1 mm measured at Gårdsjön was 17% of the total ground vegetation root biomass found by Havas and Kubin (1983). The assumed turnover time of 50% per year of total root biomass of the ground vegetation may be an overestimate. On the other hand, a 100% per year turnover of the measured tree fine root biomass <1 mm may be an underestimate, as this is only 1/3 of the fine root biomass included in the active plant pool. The uncertain size of the root biomass affects the estimates of litter production. The uptake of N by plants is calculated as the sum of litterfall plus net accumulation of N in the plant pools. The uptake of N, in turn, affects the calculated gross mineralisation rate. A good estimate of the litter flux is, thus, critical in modelling N cycling and N transformation within the forest ecosystem.

The transfers of C and N from the LOM to the ROM pool in the MERLIN model are determined by the litter input, accumulation of C and N in the pools and decomposition of organic matter in the LOM pool. Limited data exist on the latter parameters for the G2 NITREX catchment. Berg *et al.* (1995) estimated accumulation of organic matter in the forest floor in various types of coniferous forests using a model which includes data for above-ground litterfall and maximum decomposition rates of litter. Between 8 and 11% of above-ground total litterfall C was accrued annually to the organic matter of the forest floor. For the Gårdsjön catchment, a build-up of 8% of the total above-ground litter amounts to 1.29 mol C m^{-2} $year^{-1}$, which equals a build-up of 25% of the total forest floor C pool between 1930 and 1990, and a build-up of 0.04 mol N m^{-2} $year^{-1}$. The modelled build-up of 0.04 mol N m^{-2} $year^{-1}$ and 0.114 mol C m^{-2} $year^{-1}$ was based on an assumed decrease in the C/N ratio and an increased mineralisation due to the increased N input from 1950 onwards. The increased mineralisation rate with increasing N input is supported by Falkengren-Grerup *et al.* (in press) who found a doubling of net N mineralisation rates of the forest floor soil from areas in southern Sweden that presently receive 120 mmol N m^{-2} $year^{-1}$ relative to soil from areas receiving 50 mmol N m^{-2} $year^{-1}$. The assumed build-up of C in the forest floor, however, may be low compared to the suggested C build-up in the models of Berg *et al.* (1995). In predictions of future trends, an increased organic matter accumulation conserves C and N in the soil, which results in a lower N leaching from the system.

Data on the annual decomposition rate of soil organic matter are available on needle litter (18% dry weight loss of brown needles) and the organic F layer (8% dry weight loss) in the Gårdsjön area (Hogervorst *et al.*, 1998). No data, however, are available for annual decomposition of the whole forest floor compartment. An estimate of the decomposition of LOM may be obtained by subtracting the estimated build-up of LOM and the transfer of organic matter between LOM and ROM (decay of LOM) from the total litter input. The mineral soil in the Gårdsjön area contains large quantities of organic C and N (Fig. 2), which suggests a relatively large movement of organic matter into the mineral horizons. The estimated maximum flux of DON at 20 cm depth in 1990 was 17 mmol m^{-2} $year^{-1}$, based on measurements of soil solution sampled at 4 plots with 12 lysimeters (Stuanes and Kjønaas, 1998). The water flux in the soil at 20 cm depth was set equal to the water flux in throughfall. If this DOM had the C/N ratio of the forest floor, then the flux of C to mineral soil would be 0.61 mol C m^{-2} $year^{-1}$. DON is commonly defined as organic N < 0.45µm, thus the sampled DON represented the small-size fractions of organic matter that may be moving through the soil profile. In addition, some transport may occur in larger pores and root channels, as well as transfer down through the profile by soil fauna. As the extent of this transport is not known, the estimated transfer of organic C and N from the forest floor LOM pool to ROM was set to approximately 10 times the flux of DON in the lysimeter water at 20 cm depth; this transfer is equivalent to 11% of the total litter input.

With these accumulation and leaching rates of organic C and N in LOM, the decomposition and gross N mineralisation amounts to 51 mol C and 1.45 mol N m^{-2} $year^{-1}$. The mean net N mineralisation rate for the G2 catchment was measured at 0.132 mol N m^{-2} yr^{-1} (Kjønaas *et al.*, 1998). Net mineralisation is the difference between gross mineralised and re-immobilised N. In the MERLIN model, the immobilisation of N in the soil is affected by external input of N as well as uptake by vegetation. Rates of net mineralisation are, thus, not available as an output parameter from the model. Tietema (1998) determined a gross-to-net mineralisation ratio of 2.4 for the forest floor of the Gårdsjön area, which indicate an *in situ* gross mineralisation of 0.31 mol N m^{-2} yr^{-1}. The measured rate, mainly the forest floor, is low compared to the estimated rate in the model and it is also low compared to a calculated rate based on uptake minus deposition. Apart from the possibility that the litter flux may be overestimated due to uncertainties in the turnover of the root biomass, a substantial mineralisation may also take place in the ROM pool. In addition, uptake numbers may include assimilation of organic N that bypasses N mineralisation (Näsholm *et al.*, 1998). The modelled gross mineralisation rate may thus represent formation of inorganic N as well as amino acid and protein N that is assimilated by the vegetation.

CALIBRATION PERIOD 1990–1996

The C, N and C/N in the plant, LOM and ROM pools were calibrated to fit the measured pools in 1990 (Table 1). For the calibration period 1990 –1996, the model indicates that very little of the added N goes to the plants. This agrees with measured N concentration in needles which show no response to N addition (Kjønaas *et al.*, 1998). No data are available for the ground vegetation. The model indicates an increase in the N content and decrease in C/N of the LOM compartment. The measurements also show a significant increase in N content of LOM, albeit somewhat smaller (Kjønaas and Stuanes, unpubl.). If the thickness of the horizons and the C content are assumed to be constant, the C/N ratio calculated from the measured N content in the LOM compartment should have decreased from 35.0 to 33.9. Such small changes in the C and N contents of large pools are difficult to measure, as an increase of only 2% C in the LOM compartment would be sufficient to store the N at constant C/N. The modelled decrease in the C/N ratio from 35 to 32 is plausible if the C content is slightly reduced and/or the major part of the incoming N is retained in LOM. Measurements indicate that during 1994, 92% of the incoming NH_4 was assimilated or transformed within the upper 5 cm, and 52% of the incoming NO_3 was immobilised within the upper 10 cm of the forest floor (Kjønaas *et al.*, 1998). The change in the N content of the ROM compartment is uncertain. Both lysimeter results (Stuanes and Kjønaas, 1998) and data from resins deployed in the bottom of soil cores (Kjønaas *et al.*, 1998) indicate increased leaching of NO_3 to the mineral horizon. No significant difference in the N content of ROM, however, was measured between 1990 and 1995. The calibrated minor increase in the N content of ROM is thus consistent with measurements.

The MERLIN model could easily be calibrated to fit the observed NO_3 output in runoff for the years 1991, 1992 and 1996 (Fig. 3, line 1.) However, the model did not manage to combine the observed output flux with the criteria of less than 0.5 mmol N m^{-2} yr^{-1} loss prior to treatment (Fig. 3, line 1.) Several factors affect the leaching of dissolved inorganic N (DIN). The amount of N applied, the hydrological status of the catchment at the time of addition, and the discharge level, are all factors of importance for the output of DIN on a short term basis (Moldan and Wright, 1998). On a long-term basis, it is the changes in major processes, such as the ratio of gross NH_4 and NO_3 immobilisation to gross mineralisation and the soil C/N ratio, that are expected to determine the leaching level (Aber, 1992). The observed increased N in runoff does not reflect the ecosystem's N status, as the forest system has had only a limited time to adapt to the sudden dramatic N addition. Bypass flow may occur during the dormant season where high N input coupled with high runoff causes concentration peaks in the NO_3-N leaching from the soil (Moldan and Wright, 1998). However, some system change has occurred, as indicated by increased NO_3 in soil solution below the major rooting zone at 40 and 70 cm depth from the fourth year of treatment (Stuanes and Kjønaas, 1998), and increasing concentrations of NO_3 in runoff over the same period . As the calibrated model (Fig. 3, line 1) was assumed to reflect the N status of the system as a whole more accurately, this calibration was used to predict future N leaching from the ecosystem.

FORECAST

The simulation indicates trends in N pools and fluxes in plants, soil and runoff compatible with independent measurements including other N experiments at NITREX sites and elsewhere. In general, these all show that most of the added N goes to LOM, that foliage shows a moderate and delayed response and that leaching is a significant path for excess N in N-rich systems receiving high N deposition (Tietema *et al.*, 1998). The results from the simulated increased N input suggests that most of the added N goes to LOM and ROM. The ROM pool reacts more slowly than the LOM pool. The steady state of the plant pool from 1990 to 2030 reflects partially an old forest with slow growth, and partially an expected gradual death of older trees in the catchment (Fig. 4a).

The predicted N leaching at ambient deposition levels suggests that the ecosystem is capable of retaining virtually all incoming N in the next 50 years (Fig. 4b). The major part of the N is retained in LOM, which results in a gradual decrease in the C/N ratio towards the C/N ratio

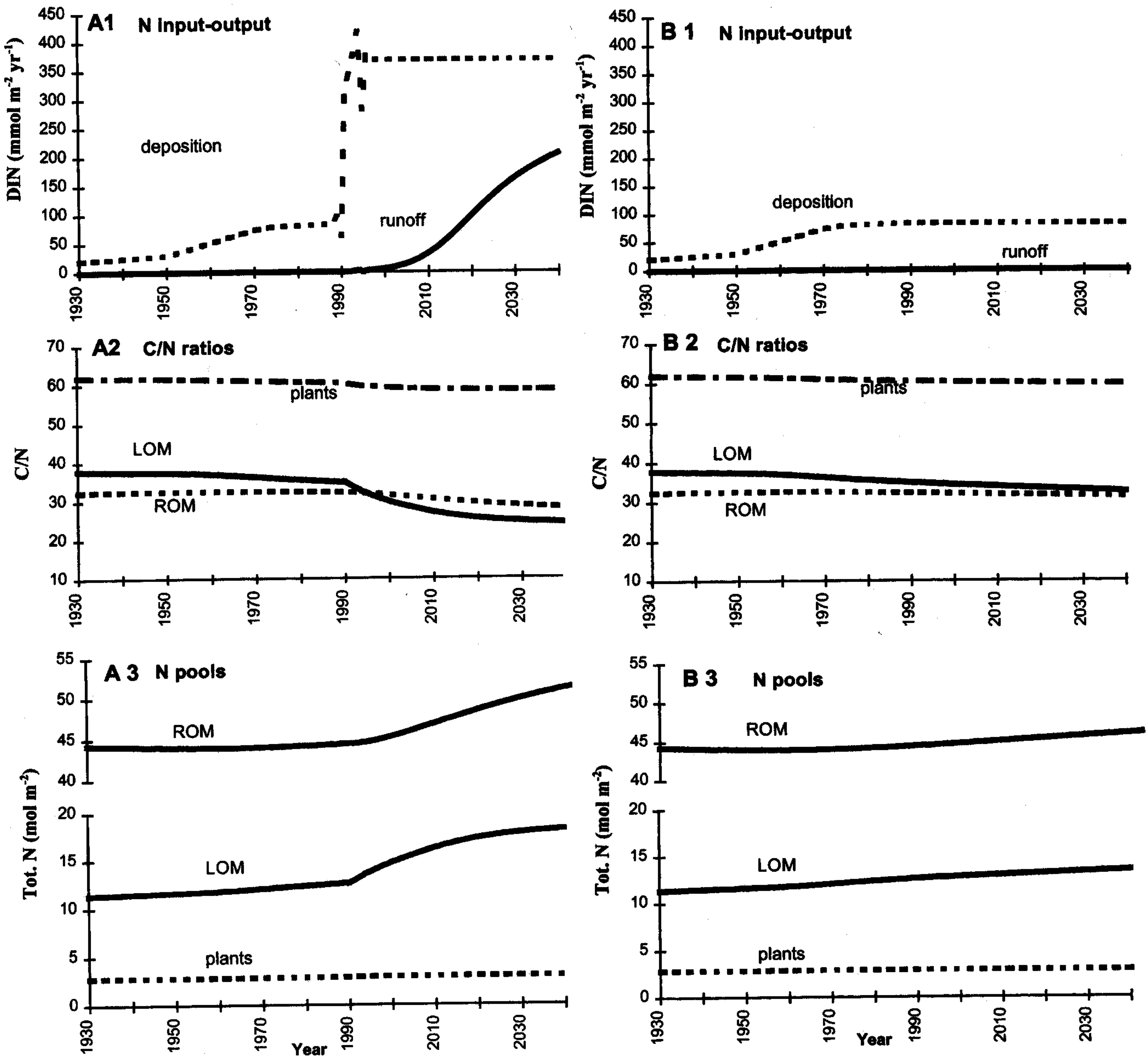

Fig. 4. *Results of MERLIN calibration and prediction for G2 NITREX catchment Gårdsjön subjected to increased N additions from 1991 (A) and constant deposition at ambient level from 1990 onwards (B). Panel 1. Deposition and runoff. Panel 2. C/N ratios in the 3 pools. Panel 3. Total N in the plant, LOM and ROM pools.*

of the ROM pool. The prediction is in agreement with the results from the NITREX experiment, where 6 years of increased N equals approximately 20–30 years of ambient N deposition level. The retention of the incoming N was measured and proved to be more than 95% over the 6-year experimental period (Moldan and Wright, 1998).

The predicted and measured retention of N was due mainly to immobilisation, which increased strongly at the onset of the N additions. A combination of the litter quality and the C/N ratio of the soil may determine the immobilisation capacity. The C/N ratio of the soil compartments is regulated by the parameters of the uptake curves, in that a given target C/N (reference) and the uptake strength (optimum C/N) govern the path of the incoming N within the ecosystem (Cosby *et al.*, 1997). A low reference C/N of the LOM and ROM pools generally implies immobilization of incoming N until the C/N ratios approach the target. The predicted rapid decrease in C/N in the LOM pool, and the slow decrease in the ROM pool from 1990 onwards (Fig. 4, A2 and B2), are to a large extent, therefore, driven by the target C/N ratios of 20 and 28, respectively, together with the steepness of the uptake curve. In the current model prediction, significant leaching occurred as the C/N ratio in LOM decreased below 28. A change in the target C/N of ROM from 28 to 23, delays the predicted onset of NO_3 leaching and reduces the runoff flux by 37% in year 2040. The simulated increased leaching losses at a C/N ratio below 28 generally follow the relation between the C/N ratio and N leaching shown by the ECOFEE database (Gundersen *et al.*, in press). The ECOFEE data, however, indicate a 'transition zone' between C/N ratio of 30 and 25 where the leaching varies among ecosystems between 7 and 179 mmol N m^{-2} $year^{-1}$. Low N leaching, therefore, falls within the trends of the ECOFEE data base, as does the currently simulated significant N leaching. The reason for the large variation in leaching from different sites with similar C/N ratios is not clear.

On a long-term basis, the C/N ratio in ROM should change slowly and reflect the quality of leaching organic matter. In Scandinavia, the C/N ratio commonly decreases with depth in the soil profile (e.g. Kjønaas *et al.*, 1992; Mulder *et al.*, 1997). Fractionation of dissolved organic matter (DOM) occurs during percolation, as the C/N of soil organic matter in the mineral horizon is generally lower than the C/N of the DOM in the forest floor. Within the European NITREX experiments, the C/N ratios of the mineral soil ranged between 18 and 38, and the C/N ratio in the mineral horizon of the two Dutch sites were 6–18 units higher than the C/N ratio of the forest floor (Gundersen *et al.*, 1998). Although the data set is too small to draw definite conclusions on the role of the mineral soil in retaining incoming N, the results indicate that the mineral horizon has limited importance in controlling the leaching of NO_3 (Gundersen *et al.*, 1998). The mineral soil N pool is large; a small change in the C/N ratio represents a lot of N. In this model simulation, the mineral horizons show a considerable capacity to assimilate DIN even with a target C/N of 28 (Fig. 4, panel A3). The relative importance of immobilization/uptake to leaching is determined by the optimum C/N. If the optimum C/N is set low (1–10), the model simulates an ongoing and increasing immobilization of N even after 50 years with increased N input at the G2 NITREX site. Potentially, the soil microflora may immobilise more than that necessary for their own growth, and this 'luxury uptake' may not be liberated until the C/N ratio has become unnecessarily low (Fog, 1988). On the other hand, temporal reductions in the assimilation rates of the microflora may cause increased NO_3 leaching, as indicated in the G2 NITREX catchment in the fourth year of treatment (Kjønaas *et al.*, 1998). Little is known about the assimilation capacity and the transformation of C and N pools in both the forest floor and the mineral horizons. Generally, the time needed for a system to change from being N-limited, indicated by high C/N in LOM, to an N-rich system, with a C/N below 25, is uncertain, and the processes that govern the transition are not fully understood.

The modelled leaching of DIN from the ecosystem increased as a result of the levelling off and slight decline in the predicted immobilisation along with an increase in the internal production of N (Fig. 5b). The decomposition/gross mineralisation rates were predicted to increase relatively rapidly with increased addition of N (Fig. 5a). Although the predicted gross mineralisation rates are difficult to verify, the measured increase in net mineralisation rates in the third year of N addition (Kjønaas *et al.*, 1998) and the doubling of mineralisation rate in areas with larger N input in Southern Sweden (Falkengren-Grerup *et al.*, in press), support the predicted trend. Temperature and moisture govern the rate of decomposition and N transformation. In addition, both N content of litter and soil inorganic N concentrations, as well as availability of substrate C, have been found to affect decomposition rate (Fog, 1988; Aber *et al.*, 1990). Berg (1986) found that increased N availability could increase the initial decomposition of the easily degradable non-lignified substances of litter, but that increased N availability may decrease the decomposition of lignin-rich organic substances. This may explain the different decomposition rates along a N deposition gradient within the NITREX project, where the relative weight loss of brown needles in the area receiving large N input was double that in areas receiving lower anthropogenic N input, while the decomposition of the organic F layer was reversed (Boxman *et al.*, 1998). Different decomposition/gross mineralisation rates have profound effects on predicted N leaching losses from forests (Fig. 6). Decomposition rates at a constant 1990 level combined with a build-up of the forest floor result in nearly 100% retention of incoming N at ambient deposition levels. An increase in the decomposition levels of, for

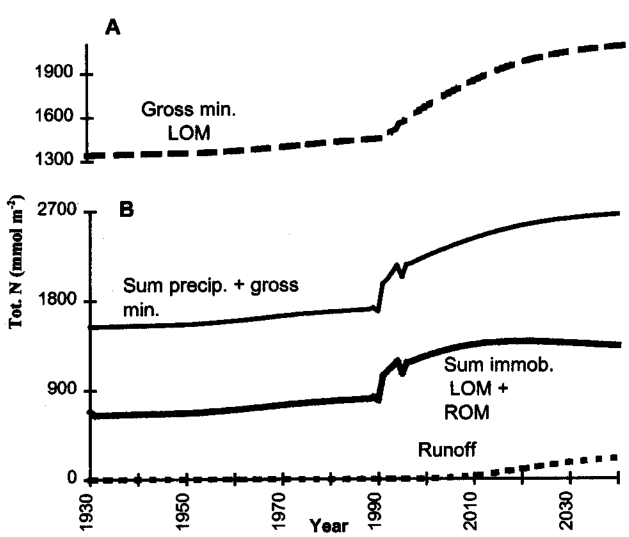

Fig. 5. *Gross mineralisation in LOM (mmol m^{-2} yr^{-1}) panel A; the sum of external and internal input of DIN as precipitation / sprinkling and gross mineralisation, the sum of immobilisation of DIN in LOM and ROM, and runoff (mmol m^{-2} yr^{-1}) in panel B for the NITREX G2 catchment subjected to increased N additions from 1991.*

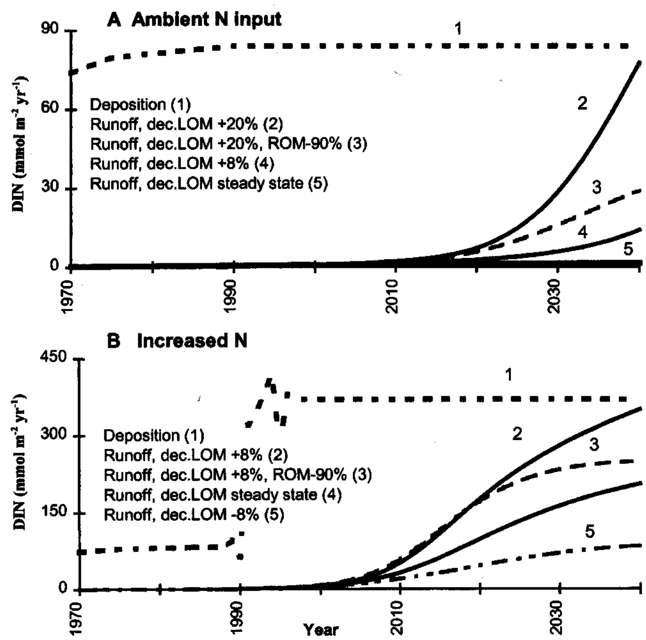

Fig. 6. *N leaching at different decomposition rates of the forest floor (LOM) with ambient N input at 1990 level (A) and increased N input starting 1991(B).*

example 8 and 20%, may increase the leaching losses of N substantially. The leaching, however, may be restrained somewhat by a parallel reduction in the old lignin-rich organic matter decomposition of the ROM horizon (Fig. 6, curve 3). With ambient deposition levels, the predicted time before an onset of N leaching may, therefore, vary between 25 and >50 years. To improve the predictability of N leaching, more information is needed on the processes that govern the C and N transformation and N retention within N-limited forested ecosystems.

Conclusions

The application of MERLIN corroborates the calibration at Aber forest (Emmett *et al.*, 1997) in that both point to the basic lack of sufficient information on C and N cycling in forests and especially the changes in pools and fluxes during cycles of forest growth and harvesting. Litter production, build-up of LOM and changes in ROM over the lifetime of a forest are poorly known. Studies such as the survey of Sitka spruce stands of different ages in Wales (Emmett *et al.*, 1993; Stevens *et al.*, 1994) are required for other major tree species such as Norway spruce and Scots pine.

The N fluxes in the model are controlled by C productivity and the C/N ratios of the organic compartments. In N-limited systems, however, the availability of N is generally the driving force that regulates the turnover rates, amount and distribution of C (Ågren *et al.*, 1991). A model based on C/N controls and C productivity, therefore, may not be valid in N-limited forest ecosystems. In addition, understanding of the processes that govern the transition from an N-limited system, indicated by high C/N in LOM, to an N-rich system, with a C/N below 25, is limited. Both the rate and capacity of N assimilation as well as the response of the C dynamics are key parameters connected to ecosystem changes. Since the knowledge of these parameters is currently inadequate, the model has a limited ability to predict excess N leaching from Scandinavian coniferous forests with high C/N ratios. The model is a useful tool for book-keeping of N pools and fluxes. It is compatible with the empirical relationships from the ECOFEE database (Gundersen *et al.*, in press), and it is an important contribution to further development of qualitative understanding of the N cycle in forests.

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References

Aber, J.D., Nadelhoffer, K.J., Steudler, P. and Melillo, J.M., 1989. Nitrogen saturation in northern forest ecosystems. *Bioscience*, **39**, 378–386.

Aber, J.D., Melillo, J.M. and McClaugherty, C.A., 1990. Predicting long term pattern of mass loss, nitrogen dynamics and soil organic matter formation from initial litter chemistry in forest ecosystems. *Can. J. Bot.*, **68**, 2201–2208.

Aber, J.D., 1992. Nitrogen cycling and nitrogen saturation in temperate forest ecosystems. *Tree*, **7**, 220–223.

Albrektson, A., 1980. Total tree production as compared to conventional forestry production. In: Structure and Function of Northern Coniferous Forests—An Ecosystem Study (T. Persson (Ed.)) , *Ecol. Bull.* (Stockholm), **32**, 315–327.

Ågren, G.J., McMurtrie, R.E., Parton, W.J., Pastor, J. and Shugart, H.H., 1991. State-of-the-art models of production-decomposition linkages in conifer and grassland ecosystems. *Ecol. Appl.*, **1**, 118–138.

Berg, B., 1986. Nutrient release from litter and humus in coniferous forest soil—a mini review. *Scand. J. For. Res.*, **1**, 359–369.

Berg, B., McClaugherty, C., Vizero De Santo, A., Johansson, M-B. and Ekbohm, G., 1995. Decomposition of litter and soil organic matter—Can we distinguish a mechanism for soil organic matter build-up? *Scand. J. For. Res.*, **10**, 108–119.

Binkley, D. and Högberg, P., 1997. Does atmospheric deposition of nitrogen threaten Swedish forests? *For. Ecol. Manage.*, **92**, 119–152.

Boxman, A.W., Blanck, K., Brandrud, T-E., Emmett, B.A., Gundersen, P., Hogervorst, R.F., Kjønaas, O.J., Persson, H. and Timmermann, V., 1998. Vegetation and soil biota response to experimentally-changed nitrogen inputs in coniferous forest ecosystems of the NITREX project. *For. Ecol. Manage.*, **101**, 65–79.

Braastad, H., 1975. *Yield tables and growth models for Picea abies.* Reports of the Norwegian Forest Research Institute, 31.9.

Canadian system of soil classification, 1978. Canada Soil Survey Committee, Subcommittee on Soil Classification. *Can. Dep. Agric. Publ.* **1646**. Supply and Services, Canada, Ottawa, Ont. 164 pp.

Clemensson-Lindell, A. and Persson, H., 1995. Fine-root vitality and distribution in three catchment areas at Gårdsjön. *For. Ecol. Manage.*, **71**, 123–132.

Cosby, B.J., Ferrier, R.C., Jenkins, A., Emmett, B.A., Wright, R.F. and Tietema, A., 1997. Modelling the ecosystem effect of nitrogen deposition: Model of Ecosystem Retention and Loss of Inorganic Nitrogen (MERLIN). *Hydrol. Earth System Sci.*, **1**, 137–158.

Dise, N.B. and Wright, R.F., 1995. Nitrogen leaching from European forests in relation to nitrogen deposition. *For. Ecol. Manage.*, **71**, 153–162.

DiStefano, J.Fco and Gholz, H.L., 1986. A proposed use of ion exchange resins to measure nitrogen mineralisation and nitrification in intact soil cores. *Commun. Soil Sci. Plant Anal.*, **17**, 989–998.

Emmett, B.A., Boxman, A.D., Bredemeier, M., Moldan, F., Gundersen, P., Kjønaas, O.J., Schleppi, P., Tietema, A. and Wright, R.F., 1998. Predicting the effects of atmospheric nitrogen deposition in conifer stands: evidence from the NITREX project. *Ecosystems*, **1**, 352–360.

Emmett, B.A., Cosby, B.J., Ferrier, R.C., Jenkins, A., Tietema, A. and Wright, R.F., 1997. Modelling the ecosystem effects of nitrogen deposition: Simulation of nitrogen saturation at a Sitka spruce forest, Aber, Wales, UK. *Biogeochemistry*, **38**, 129–148.

Emmett, B.A., Reynolds, B., Stevens, P.A., Norris, D.A., Hughes, S., Görres, J. and Lubrecht, I., 1993. Nitrate leaching from afforested Welsh catchments—interactions between stand age and nitrogen deposition. *Ambio*, **22**, 386–394.

Falkengren-Grerup, U., Brunet, J. and Diekmann, M., In press. Nitrogen mineralisation in deciduous forest soils in south Sweden in gradients of soil acidity and deposition. *Environ. Pollut.*

Fog, K., 1988. The effect of added nitrogen on the rate of decomposition of organic matter. *Biol. Rev.*, **63**, 433–462.

Gundersen, P., Emmett, B.A., Kjønaas, O.J., Koopmans, C.J. and Tietema, A., 1998. Impact of nitrogen deposition on nitrogen cycling in forests: a synthesis of NITREX data. *For. Ecol. Manage.*, **101**, 37–55.

Gundersen, P., Callesen, I. and de Vries, W., In press. Nitrate leaching in forest ecosystems is related to forest floor C/N ratios. *Environ. Pollut.*

Havas, P. and Kubin, E., 1983. Structure, growth and organic matter content in the vegetation cover of an old spruce forest in Northern Finland. *Ann. Bot. Fennici.*, **20**, 115–149.

Hogervorst, R.F., Zoomer, H.R. and Verhoef, H.A., 1998. Decomposition and microflora changes in spruce-forested catchments at Gårdsjön following reduced acid deposition. In: *The Gårdsjön roof project: Experimental reversal of acid rain effects* (H. Hultberg and R. Skeffington (Eds.)). Wiley, Chester UK, 293–306.

Johnson, D.W., 1992. Nitrogen retention in forest soils. *J. Environ. Qual.*, **21**, 1–12.

Kjønaas, O.J., Stuanes, A.O. and Huse, M., 1992. Soils and soil solution. In: *NITREX project-Gårdsjön. Status report for 1990–91* (N.B. Dise and R.F. Wright (Eds.)). Oslo, Norwegian Institute for Water Research, **2**, 23–30.

Kjønaas, O.J., Stuanes, A.O. and Huse, M., 1998. Effects of weekly nitrogen additions on N cycling in a coniferous forest catchment, Gårdsjön, Sweden. *For. Ecol. Manage.*, **101**, 227–249.

Klemedtsson, L., Klemedtsson, A.K., Moldan, F. and Weslien, P., 1997. Nitrous oxide emission in Swedish forest soils in relation to liming and simulated increased N deposition. *Biol. Fert. Soils*, **25**, 290–295.

Marklund, L.G., 1988. *Biomass functions for pine, spruce and birch in Sweden.* Sveriges Lantbruksuniversitet, Institut for Skogstaxering, 45, 73 pp.

Moldan, F., Hultberg, H., Nyström, U. and Wright, R.F., 1995. Nitrogen saturation at Gårdsjön, SW Sweden, induced by experimental addition of nitrogen. *For. Ecol. Manage.*, **71**, 89–97.

Moldan, F. and Wright, R.F., 1998. Changes in runoff chemistry after five years of N addition to a forested catchment at Gårdsjön, Sweden. *For. Ecol. Manage.*, **101**, 187–197.

Mulder, J., Nilsen, P., Stuanes, A.O. and. Huse, M., 1997. Nitrogen pools and transformations in Norwegian forest ecosystems with different atmospheric inputs. *Ambio*, **26**, 273–281.

Mylona, S., 1996. Sulphur dioxide emissions in Europe 1880–1991 and their effect on sulphur concentrations and deposition. *Tellus*, **48B**, 662–689.

Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Högberg, M. and Högberg, P., 1998. Boreal forest plants take up organic nitrogen. *Nature*, 392, 914–916.

Nygaard, P.H., Huse, M. and Stuanes, A.O., 1993. Vegetation. In: *NITREX project-Gårdsjön. Status report for 1991–92: the first year of treatment* (R.F. Wright (Ed.)). Norwegian Institute for Water Research, Oslo, p. 33–38.

Olsson, B., 1985. Land-use history of the Lake Gårdsjön area, SW Sweden. *Ecol. Bull.* (Stockholm), **37**, 35–46.

Olsson, B., Hallbäcken, L., Johansson, S., Melkerud, P-A., Nilsson, S.I. and Nilsson, T., 1985. The Lake Gårdsjön area—physiographical and biological features. *Ecol. Bull.* (Stockholm), **37**, 10–28.

Persson, T. and Wirén, A., 1995. Nitrogen mineralisation and potential nitrification at different depths in acid forest soils. *Plant Soil*, **168**, 55–65

Simpson, D., Olendrzynski, K., Semb, A., Støren, E. and Unger, S., 1997. *Photochemical oxidant modeling in Europe: multi-annual modeling and source-receptor relationships.* EMEP/MSC-W report 3/97, Norwegian Meteorological Institute, Oslo, Norway, 75 pp.

Sogn, T., Stuanes, A.O. and Abrahamsen, G., 1997. *Accumulation of N—variations connected to stand age and N input.* (In Norwegian, English summary). Report nr. 10/97, Norges Landbrukshøgskole, Institutt for jord- og vannfag, Ås Norway, 5–12.

Stevens, P.A., Norris, D.A., Sparks, T.H. and Hodgson, A.L., 1994. The impacts of atmospheric N inputs on throughfall, soil and stream water interactions from different aged forest and moorland catchments in Wales. *Wat., Air Soil Pollut.*, 73, 297–317.

Stoddard, J.L., 1994. Long-term changes in watershed retention of nitrogen: its causes and aquatic consequences. In: *Environmental Chemistry of Lakes and Reservoirs* (L. Baker (Ed.), p. 223–284. Advances in Chemistry Series, No. 237, American Chemical Society, Washington, DC.

Stuanes, A.O., Andersson, I., Dise, N.B., Hultberg, H., Kjønaas, O.J., Nygaard, P.H. and Nyström, U., 1992. *The NITREX project (Nitrogen saturation experiments).* (N.B. Dise and R.F. Wright (Eds.)). Brussels, Commission of the European Communities. 2, 24–34.

Stuanes, A.O. and Kjønaas, O.J., 1998. Soil solution effects after four years addition of NH_4NO_3 to a forested catchment at Gårdsjön, Sweden. *For. Ecol. Manage.*, **101**, 215–226.

Tietema, A., 1998. Microbial carbon and nitrogen dynamics in coniferous forest floor material collected along a European nitrogen deposition gradient. *For. Ecol. Manage.*, **101**, 29–36.

Tietema, A., Emmett, B.A., Gundersen, P., Kjønaas, O.J. and Koopmans, C.J., 1998. The fate of 15N-labelled nitrogen deposition in coniferous forest ecosystems. *For. Ecol. Manage.*, **101**, 19–27.

Wright, R.F., Brandrud, T.E., Clemensson-Lindell, A., Hultberg, H., Kjønaas, O.J., Moldan, F., Persson, H. and Stuanes, A.O., 1995. NITREX project: ecosystem response to chronic addition of nitrogen to a spruce-forested catchment at Gårdsjön, Sweden. In: *Effects of Acid Deposition on the Terrestrial Environment of Sweden* (H. Staaf and G. Tyler (Eds.)). Ecological Bulletins (Copenhagen) 44, 322–334.

Wright, R.F. and van Breemen, N., 1995. The NITREX project: An introduction. *For. Ecol. Manage.*, 71, 1–6.